Comments on the Phylogeny and Biogeography of Antiarchs (Devonian Placoderm Fishes), and the Use of Fossils in Biogeography

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A new cladogram for 24 antiarch genera based on 40 synapomorphies unites the bothriolepidoids and sinolepids as sister groups. Together with asterolepidoids these form a major group of advanced antiarchs (the Euantiarcha), characterized by an armoured pectoral fin with complex proximal and distal joints. The yunnanolepids from south China are a plesiomorph sister group of euantiarchs, and the most primitive known representatives. The known distribution of these 24 genera suggests that a few (e.g. *Bothriolepis*) had different dispersal capabilities from the majority of antiarchs. An attempted designation of areas of origin for the major subgroups gives the following: asterolepidoids, an area excluding south China; bothriolepidoids plus sinolepids, south China, or south China plus Australia; yunnanolepids, south China; euantiarchs and antiarchs, cosmopolitan. In considering the types of evidence used in developing biogeographic hypotheses involving Palaeozoic fossils, it is suggested that biostratigraphic data may indicate changing barriers with time, and palaeogeography based on current geological theory is essential to relate modern fossil occurrences to past geography. Biogeographic problems concerned with taxon and area relationships should be delineated such that one of three sets of initial conditions can be specified: either there was a common ancestral biota in the areas under consideration, or one or more of the areas lacked any biota, or differences in fauna and flora between areas was at such high taxonomic levels as to be irrelevant to the problem being investigated. Assumptions about appropriate initial conditions may be influenced by geological theory. Arguments that the progression rule of Hennig is unfalsifiable, and assumes a complete fossil record, are rejected. In certain cases either a vicariance or a dispersal explanation may be indicated, using the distribution pattern of a single group, and geological theory of the areas concerned, but neither possibility can be conclusively refuted. Since this is also the case when whole biotas are investigated, it is suggested that the method of analysis outlined by Platnick and Nelson (1978) is more appropriately termed 'pattern' biogeography. The notion that vicariance is a preferred explanation, because dispersal explanations are unfalsifiable, results from the influence of geological theory (super-continent breakup) in the appraisal of modern distribution patterns. This would not necessarily apply in Palaeozoic times, where dispersal may have been a predominant cause of disjunct distributions. In such cases the same method of analysis is applicable, but an assumption that there was a common ancestral biota can be replaced by an assumption that there was a centre of origin for the taxa in question.

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INTRODUCTION

The antiarchs are an early order of jawed fishes belonging to the Placodermi, which attained a wide distribution during Middle and Late Devonian time. One genus, *Bothriolepis* Eichwald, is known from the Late Devonian of Britain, Belgium, Greenland, the Baltic area and the Russian platform, Siberia, Kazakhstan, China, Ellesmere Island, Canada, and the eastern and western United States in the northern hemisphere, and Australia and Antarctica in the southern hemisphere. Only from Africa and South America are Devonian antiarchs not yet known, although one un-

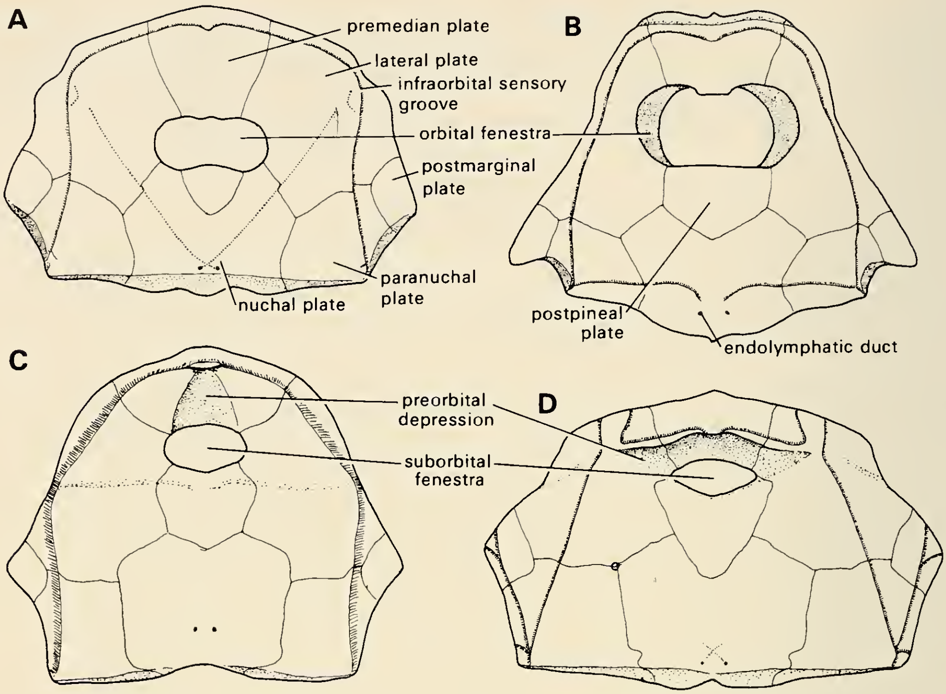

Fig. 1. Skull roof patterns for representatives of the four major antiarch subgroups. **A,** *Bothriolepis* (after Stensiö, 1948); **B,** *Asterolepis* (after Karatajute-Talimaa, 1963); **C,** *Sinolepis* (after Liu and Pan, 1958; and Long, 1983); **D,** *Yunnanolepis* (after Zhang, 1978). Not to scale.

confirmed report from Argentina (Frenguelli, 1951:86) awaits further investigation. The genus *Bothriolepis* (Fig. 1**A**) is the most widespread known placoderm, being represented by over fifty named species (e.g. Denison, 1978). By way of contrast the earliest known antiarchs, which belong to the primitive suborder Yunnanolepidoidei (Fig. 1**D**), apparently occur only in Siluro-Devonian strata in south China, where they form a major component of a highly endemic fauna of early gnathostomes defining the so-called 'south China Province'.

Their cosmopolitan distribution in the Late Devonian and restriction to the south China region in the earliest Devonian, and their predominant occurrence in apparently non-marine sediments, has made the antiarchs a group of some interest in biogeographic studies. In a previous discussion of the biogeography of Devonian vertebrates (Young, 1981), I proposed a cladogram of the major subgroups of antiarchs as a basis for preliminary biogeographic analysis. Since then new forms have been described from Iran (Janvier and Pan, 1982) and Australia (Young, 1983, 1984), and the former authors (also Long, 1983) have presented more detailed assessments of antiarch interrelationships. The purpose of the present paper is to present in detail my own view of antiarch interrelationships, and to consider further some aspects of their distribution in the light of more recent discoveries. This leads to a more general discussion of some methodological problems regarding the use of fossils in palaeobiogeography which have attracted comment in recent papers on vicariance biogeography (e.g. Nelson and Rosen, 1981).

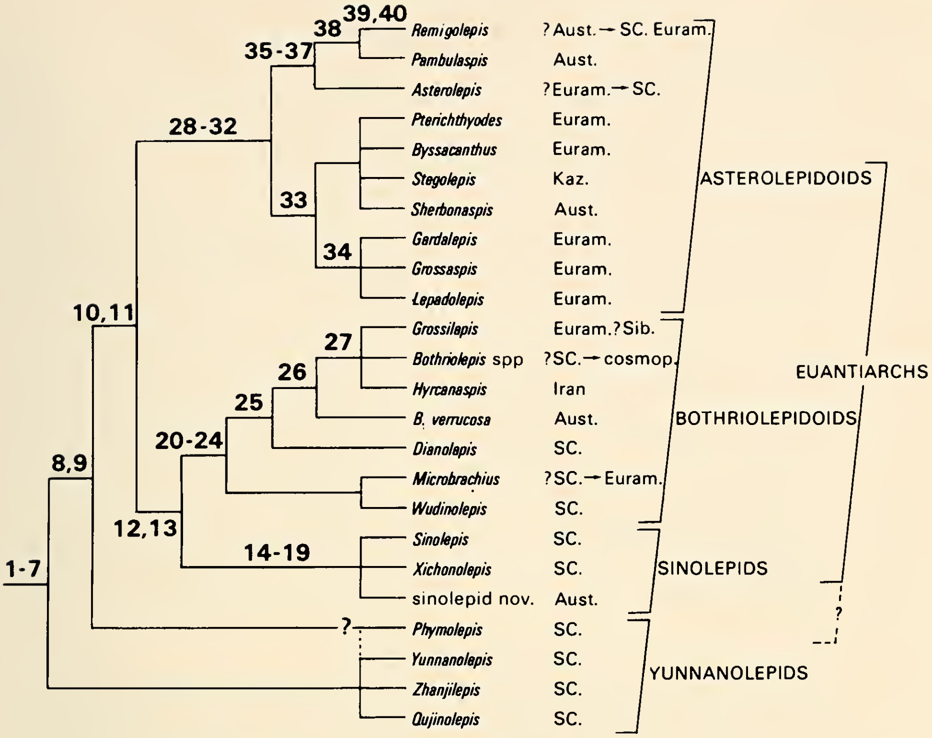

Fig. 2. Scheme of interrelationships for antiarchs, based on 40 shared derived characters (synapomorphies), with known distribution for each genus summarized on the right (arrows indicate presumed dispersal). For discussion of synapomorphies see text.

ANTIARCH INTERRELATIONSHIPS

There are several current opinions regarding the relationships of antiarchs as a group to other groups of placoderms. One viewpoint (Denison, 1975, 1978; Miles and Young, 1977; Young, 1979, 1980) is that their closest placoderm relatives are the euarthrodires, with which they share an elongate box-like body armour which completely enclosed the pectoral fin base in dermal bone. An alternative hypothesis (Goujet, 1984) assumes that this resemblance was the result of parallel evolution, and that antiarchs are instead immediately related to some palaeacanthaspids (a grade group), with which they share nasal openings in a dorsal position near the midline, with a large premedian plate forming a dermal rostrum to the skull.

For present purposes, I have assumed the first hypothesis to be correct. In the following analysis this assumption affects certain decisions of character polarity using the technique of outgroup comparison. In particular, under Goujet's alternative hypothesis a different set of antiarch synapomorphies would apply instead of those listed below (characters 1-7), and some other characters would be subject to alternative interpretation.

My view of the interrelationships of various antiarch taxa is expressed in a cladogram for all genera for which there is reasonable knowledge of morphology (Fig. 2). The 40 shared derived characters (synapomorphies) on which it is based are listed below in groups of characters defining the antiarchs and their major subgroups.

antiarch synapomorphies

1) incorporation of an extra (probably posterior) median dorsal element in the trunk-shield.

2) loss or fusion of the anterior lateral plate, so that the pectoral fenestra is bounded only by the spinal (if present) anteriorly and laterally, and elsewhere by the anterior ventrolateral (see Zhang, 1980).

3) development of a lateral plate in the head-shield, bounding the orbits laterally.

4) concomitant with 3), and associated with dorsal migration of the orbits toward the midline, the reduction and loss (and/or fusion with surrounding bones) of the preorbital and postorbital plates.

5) reduction of sclerotic plates to three in number (see Hemmings, 1978: 18).

6) associated with posterior migration of the nares to a dorsal midline position, the reduction and loss (and/or fusion with other plates) of the postnasal element (in *Yunnanolepis* the anterior portion of the lateral plate bounds the naris laterally, as does the postnasal in some primitive euarthrodires).

7) concomitant with (6), the enlargement of an internasal element (or appearance of a new unpaired dermal element in the skull), to form the premedian plate.

euantiarch synapomorphies

8) development of small dermal plates covering the pectoral appendage.

9) development of the processus brachialis, foramen axillare and associated structures involved in a complex proximal dermal articulation between the pectoral fin and shoulder girdle.

10) development of a distal joint in the pectoral fin.

11) loss of interolateral and spinal plates, assuming these are present in *Yunnanolepis* (Zhang, 1980: pl. 5, fig. 3) in addition to paired semilunars (Zhang, 1978: fig. 1B). Alternatively, the semilunar may be a modified interolateral.

synapomorphies of sinolepids and bothriolepidoids

12) elongation of the proximal part of the pectoral fin, with reduction of dorsal central plate 2 (poorly known in *Sinolepis*).

13) posterior ventrolateral and posterior lateral fused to form (or replaced by) a single plate (*sensu* Janvier and Pan, 1982; status in sinolepids uncertain, alternatively a bothriolepidoid synapomorphy).

sinolepid characters

14) posterior ventral pit and process lie behind the crista transversalis interna posterior (status uncertain, as this condition may be primitive for placoderms generally).

15) anterior and posterior ventrolateral plates much reduced both laterally and ventrally: median ventral plate, if present, very large and subrectangular in shape (A. Ritchie, *pers. comm.*).

16) parallel-sided posterior median dorsal plate.

17) anterior median dorsal overlaps posterior dorsolateral or mixilateral plate over the length of their common suture.

18) loss of lateral corners and development of wide anterior margin on anterior median dorsal plate (the condition in *Xichonolepis* compared to *Sinolepis* shows that these features developed within the group).

19) occipital commissure on nuchal and main lateral line of trunk armour reduced or absent.

bothriolepidoid synapomorphies

20) posterior ventrolateral and posterior lateral fused to form (or replaced by) a single plate (assuming absence or separate development in sinolepids; cf. character 13 above).

21) posterior dorsolateral overlaps anterior median dorsal over most of their common suture.

22) anterior median dorsal with broad anterior margin.

23) unpaired semilunar plate.

24) posterior oblique cephalic pitline developed.

bothriolepid characters

25) preorbital depression replaced by preorbital recess.

26) nuchal with orbital facets, and postpineal excluded from contact with the lateral plate.

27) enlarged foramen axillaris.

asterolepidoid synapomorphies

28) short obstantic margin facing posteriorly.

29) posterolaterally extended postmarginal plates.

30) enlargement of suborbital and orbital fenestrae to incorporate the preorbital depression.

31) loss of anterior ventral pit and process on anterior median dorsal plate.

32) mental plates meet in the midline.

asterolepid characters

33) high, short trunk-shield.

34) similar dorsal spongiose layer in dermal bone of trunk-shield (see Gross, 1965).

35) nasal openings on anterior margin of broad rostral plate.

36) unornamented shelf, premedian notch, and rostrocaudal groove on premedian plate.

37) reduced endocranial postorbital processes.

38) pronounced postpineal thickening.

39) loss of posterior ventral pit and process on posterior median dorsal plate.

40) loss of distal joint, and ventral central series of plates, in pectoral fin.

Regarding the interrelationships of the four major antiarch subgroups this new scheme differs from previous arrangements (Young, 1981; Janvier and Pan, 1982; Long, 1983) in that sinolepids and bothriolepidoids are placed as sister groups. Otherwise the major groupings are strengthened with additional synapomorphies, although there are some minor changes. *Microbrachius* and *Wudinolepis* are included as stem bothriolepidoids, following Janvier and Pan (1982; also Hemmings, 1978; cf. Young and Gorter, 1981; Long, 1983). The idea of Janvier and Pan (1982: fig. 11) that there are two differently derived types of mixilateral plate in antiarchs is incorporated, and the arrangement of plates in the proximal segment of the pectoral fin in asterolepidoids is assumed to be primitive, and that in bothriolepids and sinolepids advanced (Young, 1984: 74). It is for this reason that the latter two groups are united as sister groups. Long (1983) has suggested that the pectoral fin of bothriolepids is more advanced in several characters, but he gave no evidence to justify interpreting reduction of the second dorsal central plate in these two groups as a parallelism. Several new synapomorphies are proposed to support the sister group relationship of *Xichonolepis* and *Sinolepis,* as previously suggested (Janvier and Pan, 1982; Long, 1983). However, Long's characterization of the group by the relatively long post-orbital division of the skull and the ventral pits beneath the dorsal trunk-shield plates is invalidated by the presence of these features in yunnanolepids. Some unpublished evidence on the morphology of sinolepids (A. Ritchie, *pers. comm.*) is incorporated, but this will be dealt with more comprehensively elsewhere, and is included here only as a basis for the biogeographic discussion. A previously proposed asterolepidoid synapomorphy (loss of the prelateral plate; see Young and Gorter, 1981: 100) has been deleted since this bone is now known to occur in *Asterolepis* (Lyarskaya, 1981).

Broad agreement on the interrelationships of the major antiarch subgroups, as now known, suggests that some meaningful biogeographic conclusions might be produced by appropriate analysis. Known distributions of the various genera are summarized in Fig. 2, but before discussing details some general questions regarding method need to be considered.

COMMENTS ON THE USE OF FOSSILS IN BIOGEOGRAPHY

Three recent publications have stimulated the discussion presented here. Patterson (1981) in particular has provided a comprehensive review of method in palaeobiogeography, and raised several important issues requiring further comment. Nelson and Rosen (1981) and Nelson and Platnick (1981) have extended the vicariance concept beyond the first detailed exposition by Platnick and Nelson (1978), which formed the basis for my previous discussion of Devonian vertebrate biogeography (Young, 1981). That discussion is now reconsidered in the light of these more recent contributions, particularly those issues relating to the distribution of fossil groups.

The evidence of biostratigraphy. In my previous discussion I suggested an origin in the Australian region for the Late Devonian placoderm *Phyllolepis,* and I argued that the early biostratigraphic appearance of this form in Australia supported this view (Young, 1981: 237). Patterson (1981: 403) has pointed out, however, that this type of argument is unreliable since any new discovery of the group in older rocks and in a different region would imply a different centre of origin. He concluded (1981: 461) that the so-called 'Matthew's rule of thumb that the site of the oldest fossils is the centre of origin' did not work for certain groups of fossil mammals, and furthermore that the general assumption on which it was based — that the fossil record is complete — is wrong. These conclusions were reached in relation to groups with living representatives, as a refutation of Keast's (1977) claim that centres of origin and dispersal cannot be reliably estimated from contemporary distributions, but only when a good fossil record is available. In this context Patterson's criticism is accepted; fossils, properly analysed within a phylogenetic framework, provide no special distributional data over and above that available from Recent forms. The fallacy of a complete fossil record on which Matthew's rule depends may be put another way — it is the fallacy that distributional (like phylogenetic) history may be read from the fossil record like pages in a book.

However, I do not believe that biostratigraphic evidence can be dismissed out of hand on the grounds that a complete fossil record is thereby assumed. In one sense — that hypotheses must be constructed on the basis of available data, however limited — this assumption is always made. Moreover, fossils can provide minimum ages for related taxa which may be critical to hypotheses postulating correlations between geological and dispersal or vicariance events (e.g. Platnick and Nelson, 1978: 3; Patterson, 1981: 453). For groups like the placoderm fishes, without modern representatives, the particular problem of a time dimension is accentuated; palaeogeography changes with time, and this may be manifested in the biostratigraphic record of any group by approximately contemporaneous presences or absences in particular regions. Rejection of all biostratigraphic data would imply that a sequential biogeographic analysis incorporating a variety of geographies through time is not possible. Patterson (1981) draws an analogy between biogeography and systematics, and in phylogenetic systematics also the use of biostratigraphic data has been rejected (e.g. Nelson, 1970). But there is an important distinction here which shows that Patterson's analogy does not apply in this case. Biostratigraphic data are widely used in traditional stratigraphic palaeontology to recognize ancestor-descendant relationships amongst fossil taxa which appear to show a consistent trend of morphological change. This 'stratophenetic' approach has been validly criticized because a complete fossil record must be assumed. Put another way, to propose one fossil species as the ancestor of another taxon, it must first be postulated that there are no unknown forms which are possible candidates for the ancestor position. The criticism of this procedure is based on the argument that we can never assert complete knowledge of a particular group. In the case of biogeography however, any assumption regarding unknown taxa is much more specific. The postulated absence of a particular taxon refers to a particular area at a particular time. Clearly, such negative evidence can never be definitely established, and some judgement must be made about the reliability of absence data in each case (Young, 1984). But the resultant predictions are precisely specified, and are testable. To return to the example of the placoderm *Phyllolepis* mentioned above, the evidence that it occurs in Devonian fish faunas of a certain age (Frasnian-Famennian) in Australia, but is absent from faunas of Frasnian age in Europe, may alternatively be presented as the hypothesis that there was an effective barrier between these areas for this taxon during the Frasnian, but not during the Famennian. This hypothesis would be refuted only by the demonstration that *Phyllolepis* had been overlooked in European vertebrate faunas of Frasnian age. In this limited sense, therefore, such biostratigraphic evidence may imply biogeographic conclusions, and they are no more dependent on assumptions of complete information than any observation about the modern distribution in space of an extant organism. The further conclusion, that the taxon originated in the area of its earlier occurrence, cannot be reached without additional evidence (see below).

The evidence of palaeogeography. That earth history and the history of the earth's biota are causally related is a basic tenet of vicariance biogeography (e.g. Croizat, 1964; Platnick and Nelson, 1978). However the degree to which geological data might influence the formulation of biogeographic hypotheses has been questioned, although such data have been put forward as potential tests of particular biogeographic models. Platnick and Nelson (1978) suggest that independent evidence of historical geology may be used to decide whether vicariance or biotic dispersal is the likely explanation of a general pattern of distribution of organisms between areas. However Patterson (1981: 455) has noted that apparent concordance between relevant geological theories and a biogeographic explanation is, on the lesson of history, hardly a reliable indicator that the explanation is correct. On the contrary, past experience suggests that biogeography has often been held back by allegiance to geological ideas current at the time.

In my 1981 paper I proposed that five distinct faunal provinces could be identified for Early Devonian vertebrates, and the delineation of these provinces was partly based on geological and geophysical evidence (e.g. palaeomagnetic data, distribution of post-Palaeozoic orogenic belts) suggesting that the areas in question were separate continental regions during the Middle Palaeozoic (Young, 1981: 226). To this extent my analysis was eclectic in applying a particular geological model about Palaeozoic continent configurations (there are others; e.g. Boucot and Gray, 1979) as a preliminary step in identifying areas of endemism based on distributional data. Contrary to the attitudes noted above I suggest that such an approach is necessary when the group concerned is known only as Palaeozoic fossils. As stated elsewhere (Young, 1984), in dealing with such groups there is no recourse to a set of reliable distributional data as is claimed to be available for some living taxa. Patterson (1981: 463) makes reference to the distribution of extant forms which 'may be regarded as completely known in many groups', but the formulation of any statement about the distribution of modern groups is dependent, if not on current geological theories, then at least on the modern result of historical geological processes; that is, on modern geography. As we go farther back in geological time, and certainly in the Palaeozoic, any notion of a particular palaeogeography is inextricably linked with global geological hypotheses, perhaps encompassing tens of millions of years of earth history. Yet, as Janvier and Pan (1982) have noted, a particular set of biogeographic relationships can apply only for a particular time; to attempt even a preliminary biogeographic analysis for Palaeozoic fossils without utilizing geological and geophysical data, and therefore without any meaningful reference to the modern geography of fossil occurrences, would be impossible. For the biogeographic analysis of living forms also, geological hypotheses cannot be excluded. The 'vastly different geological story' (that is, an unchanging geography) referred to by Patterson (1981: 455) was more of an axiom than a theory. Rejection of that axiom, and acceptance of the idea that completely different continental distributions have occurred in the past, has permitted the development in historical geology of competing hypotheses, which must influence our comprehension of, and approach to, the distributional aspects of biological data (see further below).

Biogeographic provinces and the evidence of faunal affinity. Ball (1976) identified an empirical or descriptive phase in biogeographic investigations as one concerned with identifying regions characterized by particular groups of organisms. It was noted however that an elucidation of the history of such regions as reflected by historical analysis of their characteristic faunas or floras is the real aim of historical biogeography. From this viewpoint, the suggestion (Young, 1981) that at least five distinct faunal provinces may be recognized for Early Devonian vertebrates, can be seen as a bringing together of empirical data for meaningful analysis. In general terms, given a pattern of geographic regions, each characterized by particular faunas or floras, two questions of relevance to palaeobiogeographers concerned with geological history and its influence can be asked. These are:

1. What criteria should be used to assess affinity or relationship between characteristic biotas defining particular geographic regions (biogeographic provinces)?
2. Having assessed such relationships, what can be inferred about the history of the areas occupied by those biotas?

The most widely used criterion of overall affinity has been based on taxa in common between areas. There are many palaeontological examples (e.g. Middlemiss, Rawson, and Newall, 1971; Hallam, 1973). Various statistical techniques or special coefficients have been employed to handle these similarity data (e.g. Sneath and McKenzie, 1973; Henderson and Heron, 1977) but as has been noted (Ball, 1976; Patterson, 1981) this is essentially a phenetic approach, an assessment of faunal similarity, but not of relationship. Nevertheless, to show that two areas share more taxa than either does with a third area is a desirable outcome of a comparative analysis of three distinctive faunas. But the inferences which may be drawn therefrom regarding 'affinity' between the areas concerned is a point of dispute. Almost without exception it has been assumed that areas with more taxa in common have had a more recent connection. This has been challenged by Platnick and Nelson (1978; see also Nelson and Platnick, 1979, 1980, 1981). They analyse a hypothetical example in which three areas result from subdivision of one original area containing a single widespread species. Allopatric speciation of the ancestral species during subdivision is assumed, to give taxa endemic to the three areas. Allowing for different dispersal capabilities, and the possibility that the barriers which subdivide the area may be effective for some taxa but not others, it can be shown that the same historical sequence of separations can result in a single species being shared between any two of the three areas (e.g. Nelson and Platnick, 1980: 340). In another graphic example (Nelson and Platnick, 1981: 56, 57), a hypothetical problem is posed involving three areas, each containing 100 species. In area A all 100 species are endemic, but in areas B and C 99 species are shared, and only one species is unique to each. By any of the usual measures or coefficients based on overall similarity, it is clear that areas B and C would be judged to show far greater affinity to each other than either shows to A. However, Nelson and Platnick argue that this analysis does not necessarily reflect the history of area interconnections. What is needed is a phylogenetic analysis of a species group with an endemic representative in each area. For example, if in such a group the species endemic to areas A and B are more closely related than either is to the endemic species of area C, this indicates a more recent interconnection between areas A and B, regardless of the fact that 99 species are shared between B and C, but not with A.

A central issue in this example is the basis on which the three areas are identified. If they are seen as areas of endemism, then areas B and C can be characterized only by the presence of one endemic species in each area. On the other hand, if the areas are initially recognized by geographic or other non-biotic criteria (for example three islands, three patch reefs separated by open water) then the fact that 99 species are distributed across two of the areas (as continuous interbreeding populations) shows that for these species at least the two areas have no separate identity. The essence of Nelson and Platnick's argument is that for these 99 species there are only two areas (A, and B + C), and therefore no problem of recency of area interconnections. They summarize their position by stating (Nelson and Platnick, 1980: 341) that 'shared (widespread) taxa . . . contribute no unambiguous information about area interrelationships'.

It is important to consider if, and how, this proposal can be reconciled with the many examples in palaeobiogeography of faunal provinces defined on overall similarity. What is to be made, for example, of the so-called Appalachian, Malvinokaffric, and Old World provinces for Early Devonian trilobites and brachiopods (e.g. Johnson and Boucot, 1973; Eldredge and Ormiston, 1979), in which widely-separated regions are united on the basis of shared widespread taxa?

For the palaeontologist, it should first be noted that the arguments just discussed are not necessarily valid when extinct species are involved. In the examples from the modern biota used by Nelson and Platnick (1979, 1980), interbreeding continuity of a widespread living species is assumed. The species is widespread with respect to regions

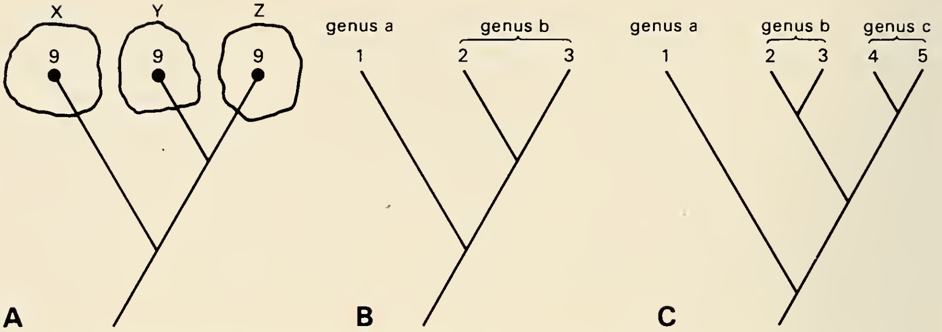

Fig. 3. **A.** Phylogenetic relationships of 27 species distributed as endemics in three areas (X, Y, Z). **B.** Three species from the three areas, related as in **A**, and classified in two genera a and b. **C.** Five species from the three areas, classified in three genera a, b, and c, each endemic to one of the areas (X, Y, Z). For discussion see text.

recognized by their endemic biotas, and it is argued that such species are not relevant to the problem of elucidating the history of those endemics and the regions they occupy. On the other hand, the distribution of an extinct species widespread with respect to modern geography may have been considerably altered by geographic change. Interbreeding continuity between modern geographic localities cannot be assumed, and to the palaeobiogeographer evidence of widespread fossil species may be of central importance in attempting to reconstruct former geographies. I refer here specifically to species, as different arguments are involved with higher taxa (see below).

The palaeobiogeographer might also question the underlying assumptions of Nelson and Platnick's argument. These seem to be 1) that speciation was allopatric; 2) that barriers effective for one species may not be effective for others; and 3) that the three areas and faunas being analysed were originally a single area with a single fauna. I know of no valid grounds for rejecting the first two assumptions, but the third might be challenged as being a special case, and therefore not generally applicable. In the 3-area example used by Nelson and Platnick (Java, Sumatra, and Borneo) it might be reasonable to suggest an originally continuous area, but there are many other examples for which there may be no evidence of original continuity. It is worth reiterating here the distinction between biotic and geographic continuity, as it is the former which is essential to Nelson and Platnick's case. There may be no evidence for geographic continuity, but the evidence for biotic continuity is simply that there are, in the areas concerned, faunas or floras which may be compared. It is the nature of this continuity which is important, and Nelson and Platnick's assumption may alternatively be expressed as the assumption that geographically distinctive biotas were emplaced by range enlargement or dispersion, and specifically not by any migration or dispersal event associated with speciation (for a discussion of the terms dispersal and dispersion, see Platnick, 1976).

This type of biotic continuity is implicit in the assumption that certain areas and their biotas comprise a particular faunal province, but it is not normally assumed by palaeobiogeographers to apply between provinces — that is, between different areas each definable on their possession of endemic taxa. The reason for this is that the faunas are seen to be different, and it is assumed therefore that dispersal across biogeographic barriers must have occurred. But, as pointed out by Platnick and Nelson (1978), there is a mechanism (vicariance) which can account for the occurrence of different taxa in different areas, and does not involve dispersal.

In assessing any scientific hypothesis it is instructive to consider possible alternatives or competing hypotheses. In the present case the specific points of difference between the vicariance approach and a more traditional provincial analysis may be brought into focus by formulating another hypothetical example in which original biotic continuity is not assumed. For supraspecific taxa this inevitably involves 'dispersal' of the type associated with speciation. We can propose three separate areas (X, Y, Z), each containing nine species (Fig. 3). None of the species is shared with the other areas. A common narrative would be that if two of the areas, say X and Y, gradually move closer together, there will be a gradual increase in shared species due to increasing dispersal between X and Y. When faunal interchange is complete, and all species are shared between the two areas, then these two provinces would cease to exist as separate entities. It is in this sense that taxa in common have been regarded as a measure of geographic proximity between areas.

However there are two major criticisms of this model, concerning first the nature of the postulated biotic distinctness of the areas under consideration, and secondly the reliability of results using taxa in common as a means of comparison. Although the three areas may be postulated as initially distinct at species level, this cannot apply for all higher taxa (unless, of course, the difference is due to the complete absence of faunas from some of the areas). The species concerned must be related in some way, and it may be that among the 27 original species specified above there are nine groups of three species, one from each of the areas, and related to each other as shown in Fig. 3**A.** This significant congruence would not come to light if taxa in common were analysed at the species level only. An analysis of genera might bring out the pattern, but this would not necessarily be the case. Consider a group of three species, one from each of the three areas, and grouped in two genera a and b (Fig. 3**B**). If their relationships are the same as in Fig. 3**A,** an analysis of genera in common would indicate closer affinity between Y and Z, the general pattern shown by the species relationships. But if there had been further speciation within areas Y and Z so that three genera (a, b, c) were recognized (Fig. 3**C**), then the absence of genera in common would again cause the relationship between endemic taxa to be overlooked if traditional methods were used. For reasons which are obvious from this example there has been much discussion in the literature (e.g. Campbell and Valentine, 1977) of taxonomic levels to be used in analysis of taxa in common. But one may ask just what special significance is to be placed on endemic taxa of high rank. Middlemiss and Rawson (1971: 201), quoting Ekman, refer to the argument that the higher the rank of an endemic taxon, the longer the isolation of that particular province. If it were true, as this implies, that rates of speciation must remain constant in different areas, then a distribution of five species in three areas as in Fig. 3**C** could not be obtained under any simple model of allopatric differentiation and/or dispersal. But there are in reality many factors which might result in more rapid speciation in one area than another (see also Nelson, 1975: 557), and it is these factors (e.g. a tectonic regime creating many different niches, a more suitable climate for the ancestral species, a lack of competition from other species) which would manifest themselves, but in no clearly-defined way, in any analysis of faunal similarity at different taxonomic levels. It is important also to note that in the example just considered (Fig. 3**B, C**), a further differentiation of endemic species within an area of endemism in no way affects, and is irrelevant to, the historical pattern of connection of that area to other areas, as evidenced by the interrelationships of taxa endemic to those areas. This is another example of confusion between the ecological and historical aspects of biogeography.

It seems, therefore, that as an alternative to hypothesizing that three endemic faunas were derived from a single ancestral fauna, we must propose that these faunas

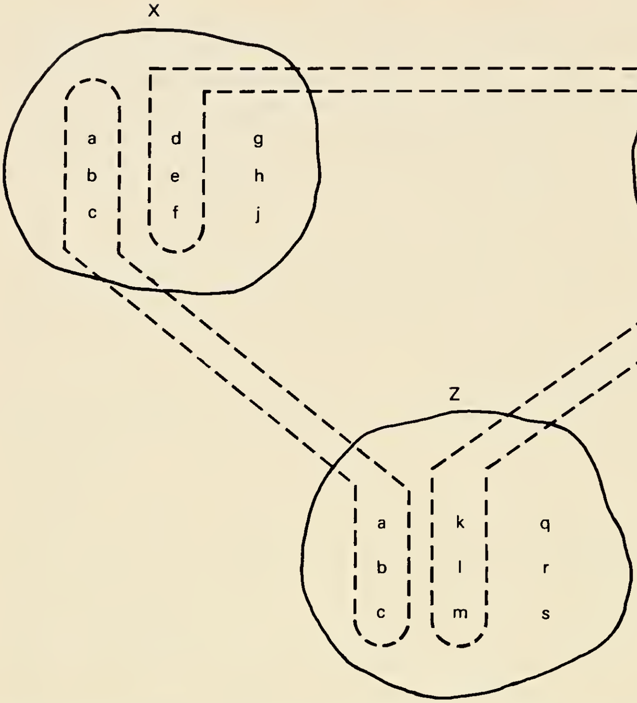

Fig. 4. Three areas (X, Y, Z) each containing nine species (taxa). Each area contains three endemic species (taxa), and each pair of areas shares three species (taxa) as indicated by the broken lines.

were originally different, although the phylogenetic relationships of the faunas, and therefore the nature of these 'differences', are not readily specified. Put another way, it is the delineation of the biogeographic problem at hand which is unclear in such an example. If the initial conditions specified (in the above case three sets of nine species, none shared between areas) are so general as to permit radically different results of analysis, then clearly the limits of investigation must be extended to incorporate those pre-existing conditions (in this example the interrelationships of species and higher taxa between areas). The judgement that assumed initial conditions adequately delimit a particular biogeographic problem may be strongly influenced by non-biological considerations such as the supposed geological history of the areas (see below).

Assuming then that appropriate initial conditions have been specified, we can further consider the reliability of results of comparing taxa in common between areas. Given the same three areas, each with nine species, the analysis of taxa in common in a situation where three species are endemic to each of the areas, and three each are shared between X and Y, Y and Z, and Z and X (Fig. 4), would not resolve any difference in affinity between the three areas. But if species interrelationships for the endemics were as shown in Fig. 5, this would be a strong indication of some special affinity between areas X and Y. Again, as in the previous case, this pattern of interconnection might be indicated by analysis of genera or higher taxa, but the nine taxa in each of the three areas (Figs 4, 5) need not be species, but could be taxa of any rank. If we were dealing with families, then those shared between two areas provide the added complication that their contained genera may be most closely related to other genera in their own area, or may have their sister groups in another area. In any

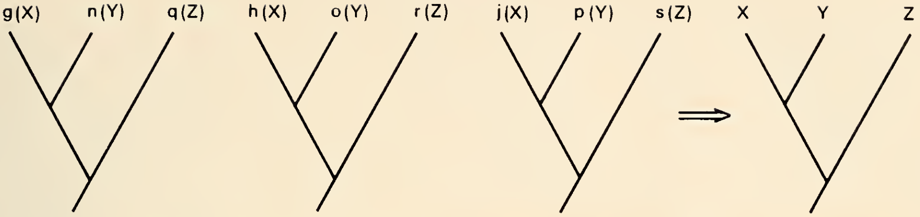

Fig. 5. Hypothetical interrelationships of the nine endemic species (taxa) of Fig. 4, and the implied pattern of interconnection (area cladogram) for the three areas X, Y, Z.

situation it is possible to analyse a set of empirical data to give results expressed either in terms of competing hypotheses, which give direction to future investigations of the problem, or as a blending of different interpretations or influencing factors, for which the future direction of investigation is unclear. In diagram form, an area cladogram might be proposed as an example of the former, and the graphic representations of Savage, Perry, and Boucot (1979: figs 6-10) would seem to be examples of the latter.

In conclusion, I suggest that an alternative to Nelson and Platnick's assumption of a common ancestral biota can only be precisely formulated if there is a complete absence of biota from one or more of the areas, or the faunas and/or floras in the areas considered are completely different at such a high taxonomic level that pre-existing interrelationships are irrelevant to the biogeographic problem being investigated. Both instances would be examples of 'vacuum biogeography', as discussed in more detail below. In other than these special cases, widespread species may be assumed to indicate faunal (reproductive) continuity between areas, and are therefore valid criteria for recognizing faunal provinces (areas of endemism). In the case of fossil species shared between widely separated areas, assumed reproductive continuity in the past may indicate subsequent geographic change, but this does not apply for supraspecific taxa, where continuity between disjunct occurrences is not reproductive (i.e. spatial), but phylogenetic (historical). A consideration of the history of connection between areas of endemism can be based only on the interrelationships of taxa endemic to those areas, and not on other more widespread taxa, which are common to two or more of those areas. These would only be informative at a higher level of analysis (involving more inclusive areas of endemism defined by such taxa). Analysis of taxa in common between areas using various taxonomic ranks may or may not give results reflecting the phylogenetic relationships of endemic taxa (and therefore the history of connection between areas), but may also give results reflecting other factors not relevant to that history. Such results cannot therefore be regarded as reliable, and alternative methods must be sought. One alternative was proposed by Hennig (1966).

Hennig's progression rule. In a short but significant paper, Nelson (1969) attempted to formalize some ideas on biogeography outlined by Hennig (1966: 133-139), and developed by Brundin (1966). Hennig's 'progression rule' provides a method by which the geographic distribution and dispersal history of a group of organisms can be inferred from the distribution of Recent taxa, given a precise hypothesis of phylogenetic (cladistic) relationships for those taxa. As an example, Nelson discussed two hypothetical sister species C and D, occurring in areas x and y, and derived from a hypothetical common ancestral species B. Nelson concluded that, without additional evidence, the most parsimonious hypothesis regarding the distribution of ancestral species B was that it last occurred in both areas x and y (Fig. 6**A**). If, however, a third species E, related to the other species as shown in Fig. 6, also occurred in area y, then

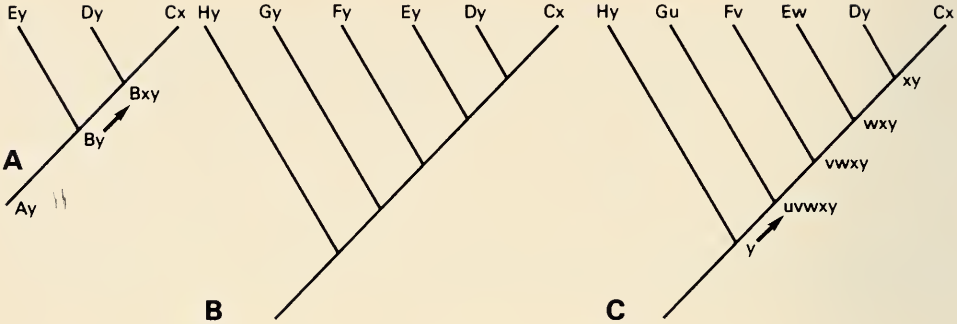

Fig. 6. Formalization of Hennig's progression rule, after Nelson (1969). **A.** Cladogram of relationships of three Recent species C, D, and E, occurring in areas x and y as indicated, with estimated distribution and dispersal (arrow) of hypothetical ancestral species A and B. **B.** Cladogram of six Recent species occurring in areas x and y as indicated. A derivation of species C from area y is indicated. **C.** Cladogram of six Recent species occurring in five areas (u-y), representing a situation where Nelson's formalization is not valid, and demonstrating that Fig. 6**B** is a special case.

the most parsimonious estimation of the distribution of the most recent common ancestor A of these three species was that it occurred only in area y, since this would require only one migration, of species B from y into x. Nelson went on to point out that if further species F, G, and H, related as shown in Fig. 6**B**, were also distributed in area y, there could be little doubt 'that the occurrence of this lineage in area x is a secondary and relatively late one' (Nelson, 1969: 244). The methodological principle employed in this analysis was subsequently paraphrased by Nelson (1973: 314):

> 'A given ancestral distribution is most parsimoniously estimated by combining descendant distributions, when they are completely different, and eliminating the unshared element when the descendant distributions are not completely different.'

In a more general statement the same idea was expressed by Brundin (1975: 70) as 'the fundamental biogeographic principle that a primitive group at least primarily is closer to the area once occupied by the ancestral species than is the comparatively derived sister group'. Regarding the circum-Antarctic distributions of chironomid midges, Brundin (1975: 21) noted that 'the marked primitiveness of the southern representatives is a demonstration of the southern origin of these subfamilies'.

The ideas of Hennig and Brundin were widely discussed and applied to various other groups (e.g. Edmunds, 1972; Cracraft, 1974). I previously expressed the view (Young, 1981: 236) that the 'progression rule' of Hennig was a valid procedure for parsimoniously estimating dispersal history using palaeontological data and phylogenetic analysis. However Hennig's ideas were also criticized on a number of grounds (e.g. Darlington, 1970), and several of these criticisms are still current. Nelson (1975) reconsidered his earlier (1969) formalization of Hennig's methods, and concluded that the procedure previously advocated was defective because it could indicate episodes of dispersal in cases when no dispersal had occurred (Fig. 7**B**). He pointed out that 'eliminating the unshared element' as previously advocated entailed an unnecessary assumption that dispersal must occur with speciation, and he proposed a modified 'rule' that 'for a given group the distribution of ancestral species can be estimated best by adding descendant distributions' (Nelson, 1975: 556). It should be noted that in Nelson's example the erroneous result attributed to defective procedure is due to failure to incorporate the basic empirical data that the problem involves three

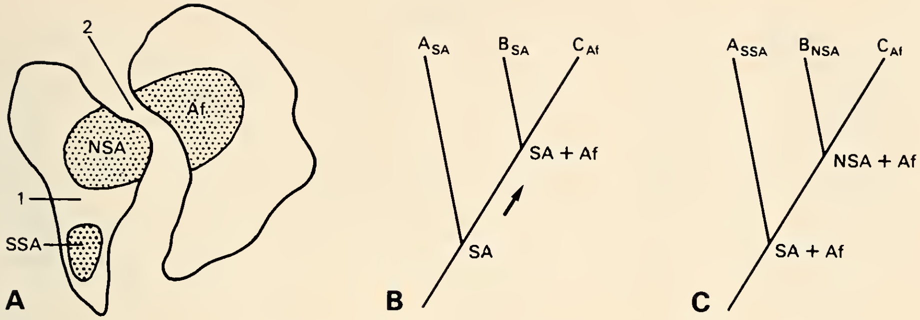

Fig. 7. **A.** Areas of endemism for three species (A, B, C) in southern South America (SSA), northern South America (NSA), and Africa (Af) respectively. The species are hypothesized to have differentiated as a result of two vicariance events, the first (1) within South America, and the second (2) between South America and Africa (modified from Nelson, 1975: fig. 1). **B.** Estimation of ancestral distribution involving dispersal when none occurred (modified after Nelson, 1975: fig. 2). **C.** Estimation of ancestral distribution which does not erroneously resolve dispersal, also using the formalization of Nelson (1969) but with separate areas of endemism for the three species properly specified.

areas, each defined by endemic species, and not two (Fig. 7**C**). Nevertheless, the acknowledgement noted above that dispersal and speciation do not necessarily go together (Croizat *et al.,* 1974; Platnick and Nelson, 1978) is an axiom of cladistic vicariance theory as it has subsequently developed. The issue of dispersal versus vicariance in a Palaeozoic context is further discussed below.

Patterson (1981) has also criticized Hennig's progression rule because of its sensitivity to incomplete fossil data as indicators of centres of origin and dispersal. He suggests (1981: 478; also Parenti, 1981: 490) that this method is reliable only if the fossil record is acknowledged to be complete, and is therefore no better than 'Matthew's rule of thumb'. But here an important difference is overlooked. Under 'Matthew's rule' (see above) the oldest known fossil can indicate a centre of origin only if it is assumed that no older fossils of that group will be found, because none exist. This assumption that the fossil record is complete has been shown repeatedly to be wrong (Patterson, 1981: 463). Under Hennig's progression rule, however, a fossil taxon providing sufficient information for its placement within a synapomorphy scheme (which may or may not include extant taxa) in effect defines a group (characterized by particular synapomorphies that fossil taxon shares with positionally apomorphic taxa within the scheme), and defines a biogeographic problem (the dispersal history of that group). No assumption of a complete fossil record is involved because newly-discovered fossil taxa qualify or not for membership of the group in question based only on their morphological characters. Furthermore, the most primitive known member of the group is in effect assessed as having the earliest separate history, and since this also is based on morphological evidence, the completeness or otherwise of the group's fossil record cannot alter this assessment. For newly-discovered taxa which lack the synapomorphies of the group in question, any resulting biogeographic inferences relate to a different problem, the dispersal history of another group which includes that new fossil. Clearly, new fossil discoveries can show previous schemes of relationship, and estimations of ancestral distribution based on them, to be wrong, but the same possibility exists regarding Recent taxa. The criticism that fossil data, ambiguous because of incompleteness, may inordinately affect conclusions regarding the dispersal history of Recent taxa, is a reasonable one only if it is claimed that all existing taxa and

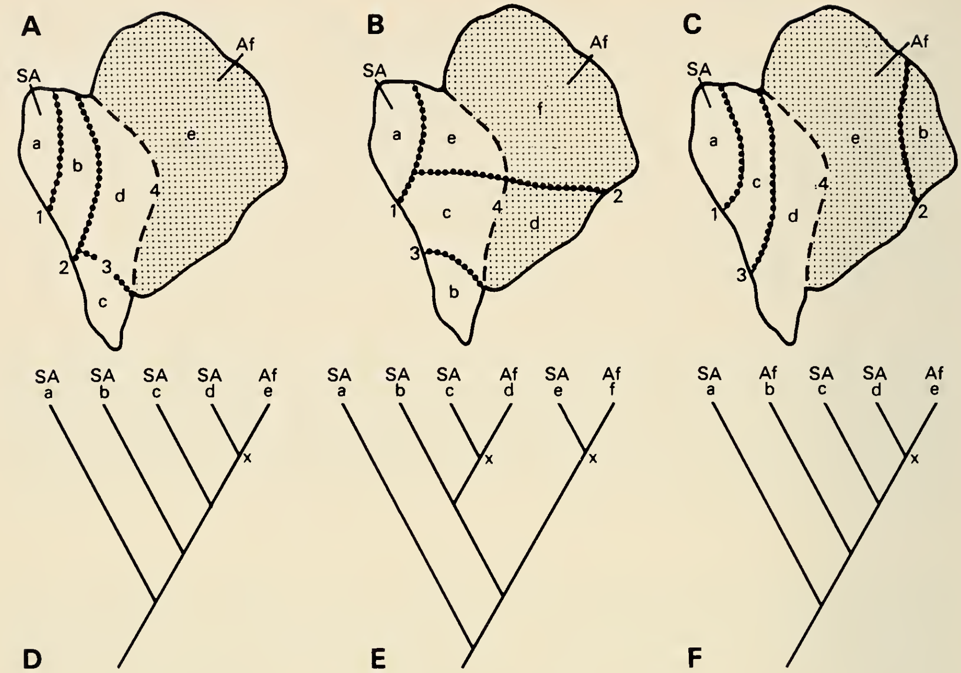

Fig. 8. Three distributions in space of vicariance events (appearance of barriers) in a region which separates into two to give a disjunct distribution for immediately related species a-f. **A** (simplified after Nelson and Platnick, 1981: 44-45). Barriers 1-3 are confined to the South American protoregion (SA), suggesting that those postdated subdivision of the area by barrier 4, and that species e dispersed across this barrier (other cladograms in which one descendant of the most recent speciation event(s) occurs in Africa can be shown to be equivalent by rotation around their nodes). **B.** One of the barriers (2) affected both African (Af) and South American protoregions, suggesting they were not yet distinct, and pointing to a vicariance explanation. **C.** One of the barriers (2) affected the African protoregion. Implications as in **B**, except that a dispersal explanation can only be excluded by adoption of additional methodological assumptions. **D, E, F.** cladograms for the species, and their distributions, resulting from the vicariance patterns of **A**, **B**, and **C** respectively; x marks the dispersal or vicariance event associated with barrier 4 (the separation of South American and African protoregions).

all Recently extinct taxa, together with their distributions, may be completely known (see above, and Patterson, 1981: 463; also Nelson and Platnick, 1981, on knowledge of Recent distributions). This criticism can hardly apply to groups known only as fossils. Patterson also suggests, in considering the example of giraffoids, that where Matthew's rule and the progression rule give conflicting results, these may reasonably be reconciled by combining the two areas concerned. But few would agree with this, and it is surely a widely-held view amongst palaeontologists that where the earliest known member of a group is not also the most primitive, then an *ad hoc* explanation would be invoked that the biostratigraphic record is incomplete (see also Patterson, 1980: 216). As just noted, the most primitive known taxon must have the earliest separate history, regardless of what is indicated by presence-absence data from the fossil record, and evidence of dispersal origins based on progression rule analysis is thus clearly superior to that based on oldest known fossil data. We assume here, of course, that the morphological evidence has been correctly assessed to recognize the most primitive known taxon.

Other comments on the Hennig-Brundin method have been made by Platnick (1981) in discussing the recent paper by Brundin (1981). Platnick elaborates the distinction between taxic and positional apomorphy, and rightly points out that the concept of taxic apomorphy, implicit in the so-called 'deviation rule' (e.g. Brundin, 1968), is a phenetic rather than a cladistic concept. He also comments on a detailed analysis of an example of amphi-Atlantic distribution presented by Brundin (1981: figs. 3.1-3.5). This is the same type of example (Fig. 6**B**) on which Nelson (1969) based his formalization of the progression rule (see above). Platnick notes that in Brundin's example the progression rule would allow the final speciation (x, Fig. 8**D**) to result either from vicariance caused by, or dispersal across, the proto-Atlantic ocean. On Brundin's argument regarding steady speciation in one area whilst no speciation occurred in the other, Platnick comments (1981:148) that 'it is more likely that the earliest barrier to divide a species widespread over two continents would appear at one end of the total area, not at the middle'. But this does not take full account of Brundin's argument, which would seem to provide a means of distinguishing vicariance from dispersal as a likely explanation in certain cases, based on the distribution pattern of a single group, and some comprehension of the geological history of the areas. Three different examples are illustrated in Fig. 8 of vicariance events in the history of a group distributed across a continental region which divides into two. Where vicariance events have occurred in both protoregions (Fig. 8**B**, **C**; Brundin, 1981: fig. 3.4) a vicariance explanation with a widespread ancestral distribution is indicated. But where (except for the most recent or equally most recent event) the history of allopatric speciation was apparently confined to one protoregion (Fig. 8**A**), it seems more likely that the disjunct distribution involving only one taxon in the other region is due to dispersal. In the sense that these speciation events might be considered attributes of a particular region, it could be concluded from the evidence of Fig. 8**A** that the differentiation of the taxa in question postdated the subdivision of the area into two. Otherwise, the confinement of these speciation events to one protoregion, before it acquired separate identity, could only be attributed to chance.

An example here is the case of the Late Devonian placoderm *Phyllolepis* discussed above. Its apparently earlier biostratigraphic appearance in Australia compared to Europe has already been mentioned. Previously (Young, 1981), the suggestion of Denison (1978) that the Antarctic form *Antarctaspis* might be a primitive phyllolepid, was considered as possible evidence for an origin of the group in east Gondwana. Further evidence is now provided with the description of new phyllolepid taxa from southeastern Australia (Ritchie, 1984; Long, 1984), which (with or without *Antarctaspis*) appear to represent a paraphyletic stem group. That the known occurrence of these primitive representatives is in the Antarctica-eastern Australia region is consistent with the hypothesis that the group evolved and diversified here before it gained access to Euramerica in the latter part of the Late Devonian. The species within the genus *Phyllolepis* can be seen as a crown group for which both regions constitute a single area. In contrast, the paraphyletic stem group is restricted to one of the regions, suggesting a barrier between them.

Thus, given certain data regarding the geographical occurrence of hypothetical barriers affecting the phylogenetic history of a particular group, inferences can be drawn on the likely explanation (vicariance or dispersal) of the distribution of that group in space. But the important point is that those situations where application of the progression rule is convincing (Figs 6**B**, 8**D**; Nelson, 1969: fig. 3) are special cases, and in other cases (Fig. 6**C**) the rule is clearly inappropriate, and obviously represents nothing more than an arbitrary assumption that attainment of a widespread distribution in the ancestral species (y, Fig. 6**C**) was by means of dispersal (associated with speciation), rather than by range enlargement. Another difficulty is that if one is prepared to admit one dispersal episode to explain the differentiation of the most recent sister species (Fig. 8**A**, **D**), then a single dispersal episode earlier in the history of the group should also be accepted. This would provide an alternative to a vicariance explanation in certain situations (e.g. Fig. 8**C**, **F**), unless a methodological rule of minimum dispersal was adopted. But consistently applied this rule would also give a vicariance explanation for the situation of Fig. 8**A**. As pointed out by Platnick and Nelson (1978), in dealing with the history of a single group neither vicariance nor dispersal explanations can be conclusively refuted, and where Hennig's rule might seem appropriate, various additional assumptions or methodological rules must be adopted (e.g. minimum parallel dispersal; minimum number of dispersal plus vicariance events, location and age of barriers as criteria for identifying discrete regions, etc.). Furthermore, in the real situation, it is unlikely that straight-forward distribution patterns of the type discussed above (Figs 6**B**, 8**D**) will be encountered, and it is likely that any appraisal of distributional biological data will be significantly influenced by knowledge of the supposed geological history of the areas (see also below). Despite these difficulties, important results have been obtained from this type of analysis (e.g. Brundin, 1966).

I suggest therefore that certain types of distribution pattern within certain geological contexts may indicate that application of the progression rule is appropriate. Clearly, it is not applicable in all cases. Thus I do not fully agree with Platnick's (1981) conclusion that the progression rule, judged by the criterion of yielding a definitive result, is no different from Darlington's (1957) rule that the centre of origin of a group is marked by the range of its most apomorphic members. Platnick also asserts that under a falsifiability criterion (Popper, 1959) the progression rule fails, since falsification depends on finding certain fossils in certain areas. He implies that any choice between the most primitive (Hennig-Brundin) or advanced (Darlington) members of a group as indicators of a centre of origin would be an arbitrary one, based only on unscientific or aprioristic criteria. But there is an important difference between these two methods, previously discussed in the literature, but worth restating. This is that under Hennig's progression rule a parsimony criterion (minimal dispersal) is employed to estimate ancestral distributions, whereas under Darlington's method an unspecified number of migratory waves are required to displace more primitive members of a group away from the evolutionary centre. Thus the former method is an analytical technique of great heuristic value, but the latter is very much a descriptive explanation of process which provides no direction for future investigations.

Turning now to Platnick's comment on falsifiability, we might also consider on this point Platnick and Nelson's earlier discussion (1978: 3-7), and comments by Patterson (1981:450-453). Because these theoretical discussions are concerned with historical explanation of a distribution of Recent taxa, which is assumed to be known, it is to be expected that the possible discovery of earlier (i.e. fossil) taxa features prominently as a potential falsifier of particular historical explanations. But it is clearly unacceptable then to use this as a ground for criticizing a certain model because of its dependence on an unreliable fossil record for falsification, as Platnick (1981: 147) has done. If the logic (Platnick and Nelson, 1978) on which this claim is based is valid, then it is clear that the falsifying taxa should play the same role in analysis whether extinct or extant, using the earlier argument of Nelson (1969: 245). As such, Platnick's (1981) claim would seem to be no more than an alternative expression of Patterson's assertion (see above) that 'Recent distributions may be regarded as completely known in many groups'. It may well be that studies in palaeontology and geology are 'subject to wide margins of error' (Platnick and Nelson, 1978: 3), and that there are certain groups in

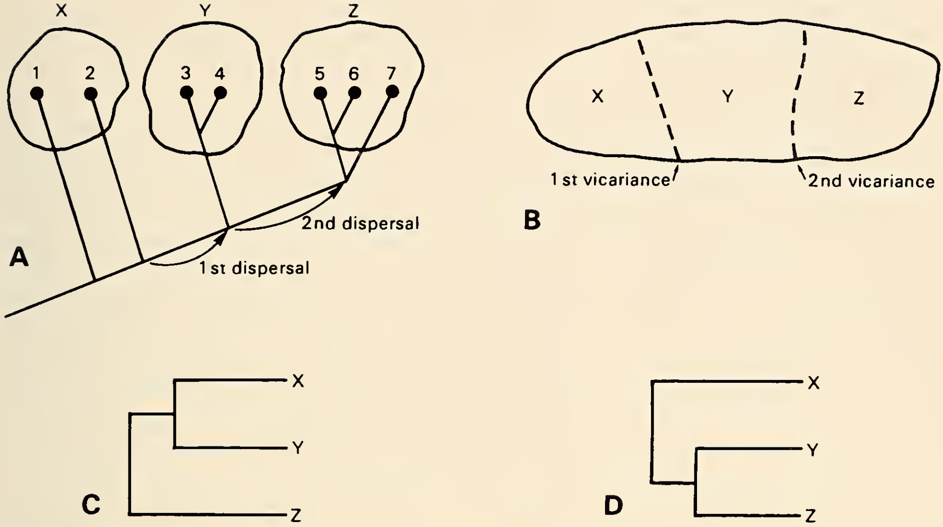

Fig. 9. Seven hypothetical species distributed in three areas (X, Y, Z), and related as shown. **A**, a dispersal explanation involving two dispersal episodes. **B**, a vicariance explanation involving two vicariance events. **C**, a similarity diagram for the areas concerned which might be derived from **A**, on the basis that X and Y are similar in possessing relatively primitive species compared to the more diverse and advanced species in area Z. **D**, an area cladogram based on **B**, consistent with the relative recency of dispersals indicated in **A**.

the modern biota whose geographic distribution may be regarded as completely known. But it surely does not follow that other branches of science are in any general or specific sense subject to less error; nor, that the relationships and distribution of monophyletic taxa amongst an appreciable number of living groups are so well understood that general conclusions can be reached regarding falsifiability of a model seeking to explain such distributions, by pointing to unreliable palaeontological data as the only means of falsification. This is tantamount to a general assumption that Recent groups are completely known. However, as is argued below (Fig. 11), it is the logic of Platnick and Nelson (1978) on which such claims are based which assumes a complete fossil record, and is therefore spurious.

In an actual situation, furthermore, any analysis of phylogenetic relationships and distribution patterns within a reasonably diverse group obviously incorporates numerous assumptions at different levels of generality, for example, empirical statements not definitely established, theoretical considerations of limited applicability, etc. The conclusions of analysis are testable as each of these assumptions is subject to further investigation. In this sense, Brundin's comments (1981: 133) about basing theoretical formulations on the analytical experience of particular cases has some relevance.

On the same issue, Patterson (1981) considers the four classes of potential falsifiers put forward by Ball (1976), and finds them to be inadequate, and to impinge primarily on the cladogram rather than the geography. But if it is assumed that a monophyletic taxon has been correctly identified, its geographic distribution is an immediately derivable empirical statement requiring no analytical procedure, and potential falsifiers concerned with that taxon could only be expected to affect the cladogram (i.e. the analytical procedure to establish monophyly). Falsifiers of the geographic part of the hypothesis would necessarily be concerned with analytical procedures related to our current comprehension of geography. In the present context this would largely involve analysis of historical geology, an aspect which Patterson argues should not be an integral part of hypothesis formulation.

To summarize, I would argue that criticism of Hennig's progression rule on two grounds (falsifiability, and assumption of a complete fossil record) cannot be sustained, and that the method as formalized by Nelson (1969) remains a valid and testable means of estimating dispersal and vicariance history, given a cladogram of interrelationships for the group concerned. If this is so, then one might ask whether the 'cladistic vicariance' method (pattern biogeography) discussed in the next section has any special merit which would justify its use in preference to Hennig's progression rule. It would seem that there is no straightforward answer to this question, because the two methods have different aims. As Platnick (1981) has pointed out, pattern biogeography attempts to discover whether areas of endemism in which many groups co-occur are interrelated to each other according to a particular pattern, which represents a summary of the phylogenetic interrelationships of some or all of the endemic groups occurring in those areas. Progression-rule biogeography, on the other hand, is in any particular example concerned with a parsimonious estimation of dispersal and vicariance history for a single group, which may not be causally related to the history of interconnection between the areas occupied by members of that group. Excluding chance dispersal, however, such analysis can provide information on area connections (Fig. 9). Dispersal events deduced from analysis can be distinguished unambiguously in terms of their chronology, and thus the relative recency of interconnections between the areas concerned can be directly inferred from the relative recency of dispersal events, as has previously been pointed out (Platnick and Nelson, 1978). From this, an area cladogram can be derived, just as can be done when a vicariance explanation is applied to similar data (Fig. 9**B**, **D**). To the extent that applications of Hennig's progression rule have dealt with dispersal histories of single groups rather than general biogeographic patterns, such applications might be regarded as deficient. But I suggest that attempts to demonstrate that the rule is unfalsifiable derive from misconceptions about the role of fossils in testing procedures, and the distinctness of biological and geological data in hypothesis formulation. These issues are best discussed in a consideration of the method of analysis proposed by Platnick and Nelson (1978).

Pattern biogeography ('cladistic vicariance'). As noted above, the biogeographic method of Platnick and Nelson (1978), here termed pattern biogeography, is concerned with whole biotas, their interrelationships, and the interrelationships of the areas they occupied. Some of the basic assumptions of this method have been mentioned above, and summarized previously (Young, 1981: 232). Under the assumption of allopatric speciation resulting either from subdivision of a continuous ancestral biota (a vicariance event), or by biotic dispersal across pre-existing barriers, it is predicted that a common pattern of interrelationships may result between taxa endemic to the areas in question. Since this pattern, as represented by a cladogram, expresses a relative chronology for the most recent common ancestors of all pairs of endemic taxa (sister groups), it may be directly converted into a cladogram of areas expressing relative recency of connection between those areas. Within the biota however there could be certain groups which were not distributed throughout the original area, did not respond to one or more vicariance events by speciating, have undergone subsequent or chance dispersal, have become extinct, have not had all their relevant species sampled, or have had their interrelationships incorrectly analysed. For such groups a simple conversion of a cladogram expressing their interrelationships into a cladogram of areas may not be valid. (According to Platnick and Nelson's analysis, however, neither extinction nor failure of some groups to respond to dispersal or vicariance events should affect the inferred area pattern). To the extent that such groups form a lesser or greater proportion of all groups investigated in relation to a particular biogeographic problem, then a general pattern will be more or less easy to recognize. A major aspect of this method of analysis is therefore concerned with comparing cladograms to establish whether they are congruent with each other in whole or in part (e.g. Nelson and Platnick, 1981). A significant number of congruent cladograms for different organisms endemic to certain areas would imply a general pattern, a general explanation of that pattern, and therefore that the resulting area cladogram was a valid one. It is possible, of course, that this type of analysis may not produce convincing general patterns because of the predominant influence of the various other factors listed above (Nelson and Platnick, 1981). The usefulness of pattern biogeography therefore awaits future analysis of test cases, since for the majority of areas of endemism, detailed information regarding interrelationships of endemic taxa required to undertake this analysis is not yet available (Nelson and Platnick, 1981).

Possible alternatives to an assumption of original biotic continuity between areas of endemism (biogeographic provinces) were discussed above, and found except in special cases to be incapable of precise formulation. On other grounds the validity of the vicariance approach has also been questioned. Previously (Young, 1981: 235) I suggested that the method may not be generally applicable to palaeobiogeography, since the vicariance analysis of Recent biotas has as its historical geological framework, according to current theory, the Mesozoic and younger fragmentation of a supercontinent (Pangaea). An assumption of primitive (Pangaean) cosmopolitanism for the biogeographic analysis of many Recent animals and plants is therefore not unreasonable. However, as noted by Brundin (1981), extensive prior dispersal must be assumed to achieve that widespread distribution. Although such aspects might be considered unnecessary and irrelevant (Croizat *et al.,* 1974; Platnick, 1981) when analysing modern distributions, they may clearly be very relevant to the palaeobiogeographer concerned with earlier periods of earth history.

It is pertinent here to comment on a point of terminology indicative of a biased approach, which has caused some confusion in the recent literature. The method of analysis outlined by Platnick and Nelson (1978) was not graced with a name, but has subsequently been referred to as 'vicariance' biogeography by Platnick (1981), and as 'cladistic vicariance' by Patterson (1981; also Young, 1981). However neither term is appropriate. Platnick and Nelson (1978: 7) concluded that 'distributional data seem sufficient to resolve a pattern of interconnections among areas that reflects their history, but not to specify the nature of those connections'. Since, according to their analysis, neither dispersal nor vicariance explanations can be unambiguously distinguished using distributional data, then why not 'dispersal' biogeography, or 'cladistic dispersal'? The answer seems to be some perceived difference in the quality of the evidence required to refute an initial assumption of dispersal, or of vicariance, as an explanation of an observed distribution. Thus, Patterson (1981: 465) writes:

> 'The dispersal interpretation is tested only by fossils of that taxon, whereas the vicariance interpretation can be tested by other taxa, fossil or living, that should have been affected by the same barriers and that therefore should show relationships congruent with those of the taxon under study. In other words, dispersal treats each taxon as an individual case, whereas vicariance is a general explanation. . . .'

But Platnick and Nelson's (1978) analysis surely shows that neither explanation of a general pattern can be conclusively falsified; postulating vicariance to explain a congruent pattern is no more general than postulating unidirectional dispersal for the

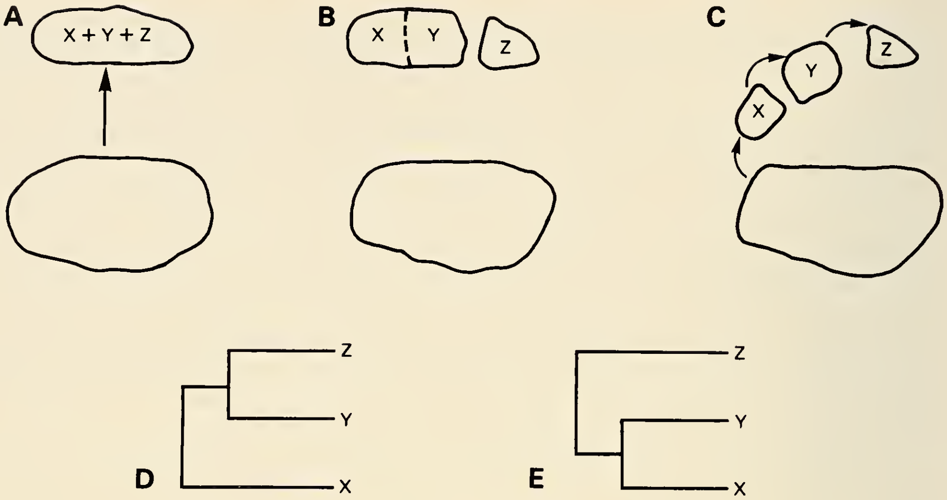

Fig. 10. An example of vicariance giving a unique area cladogram, and of directional biotic dispersal giving a different general pattern of area relationships. **A**, dispersal of founding species onto a newly-formed island (X + Y + Z). **B**, subdivision of this area, causing allopatric speciation. **C**, change in area interdistance, resulting in step-wise dispersal into the three new areas (arrows). **D**, general area cladogram for dispersing species. **E**, unique area cladogram for vicariating species.

same groups showing this pattern. Chance dispersal may be identifiable by a unique pattern, but no purely biological criteria have been proposed for distinguishing biotic vicariance from biotic dispersal as an explanation of a general pattern. And of course a unique incongruent cladogram could be the result of a single case of vicariance within a general pattern resulting from directional biotic dispersal (Fig. 10). It is unclear therefore why it is deemed necessary to demonstrate the non-testability of Brundin's methods, which were after all concerned with congruent patterns amongst three subfamilies of chironomid midges, and a geological area cladogram (e.g. Nelson and Platnick, 1981: 478). As pointed out above, the arguments of Platnick (1981) and Patterson (1981), that dispersal explanations cannot be falsified because a complete fossil record is assumed, can hardly be taken seriously when based on analysis of a theoretical example where interrelationships and distribution of the Recent taxa are taken as given; that is, where complete knowledge of those Recent taxa is assumed. Looking more closely at this theoretical example (Platnick and Nelson, 1978: fig. 1), and applying the methodological rule that fossil taxa should be treated in the same way as living taxa, it would seem that the falsifying widespread fossil taxon must be regarded either as irrelevant to this problem of area relations (Fig. 11**B**), or else as the most recent common ancestral species of the three extant taxa. Thus, it is this particular argument which assumes a complete fossil record (in which actual ancestral species can be recognized), and not the dispersal model itself. Similar arguments could be developed regarding falsification of a vicariance explanation using fossil taxa, and similar difficulties would be encountered. The reason is that the differences between the two models are concerned with the distribution of hypothetical ancestral species, which can only be known through the distribution of their descendants (the same in each case).

If we wish, therefore, to compare the testability of dispersal and vicariance interpretations of a distribution of three related taxa in three areas on its own merits (that

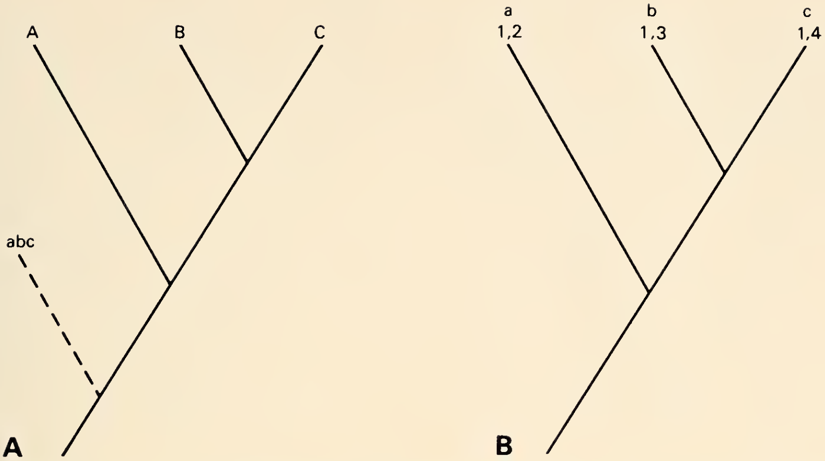

Fig. 11. **A**. Three taxa (A, B, C) distributed in three corresponding areas (a, b, c), and a widespread fossil taxon (dashed line) related as shown (after Platnick and Nelson, 1978: fig. 1.5). **B**. The same example, showing the distribution of the four taxa of A (1-4) in the three areas (a, b, c). The fact that taxon 1 is fossil demonstrates only an extinction event. Whether living or extinct, this taxon is distributed in all three areas, and is therefore irrelevant to the question of the history of interconnection of those areas.

is, not in relation to other groups occurring in the areas), we must assume incomplete knowledge of both Recent and fossil taxa relevant to the problem, and consider predictions regarding the discovery of new related taxa (extant or extinct) in the three areas. One example concerning new taxa within the crown-group (Patterson, 1981: 461) is given in Fig. 12. Another, concerning stem-group taxa, was discussed above (Fig. 8). Compared in this way, I suggest that vicariance and dispersal explanations cannot be differentiated in terms of their falsifiability. Alternatively, if we wish to compare the testability of dispersal and vicariance interpretations of the same distribution in terms of the distribution pattern of other taxa endemic to these areas, we can again consider predictions derivable from each model. Regarding a dispersal explanation, Platnick and Nelson (1978: 4) state that because 'dispersal capabilities of these organisms may or may not be similar to those of other groups, we can make no predictions about what patterns other groups that occupy these areas might show'. Equally however, vicariance events causing differentiation of the taxa in question under a vicariance explanation may or may not affect other species in the same way (e.g. Nelson and Platnick, 1980), so again we can make no predictions about what patterns other groups might show. Compared in this way, I again suggest that vicariance and dispersal explanations cannot be differentiated in terms of their falsifiability.

It is for these reasons that I use the term 'pattern biogeography' for a method of analysis (Platnick and Nelson, 1978) which acknowledges that distributional data are sufficient only to retrieve a biogeographic pattern, but not the cause of that pattern. The belief that vicariance is a preferred explanation, and attempts to justify that belief by claiming that dispersal explanations are unfalsifiable, is perhaps a holdover from earlier discussions in which the vicariance explanation was totally supported (e.g. Croizat, Nelson and Rosen, 1974; Nelson, 1975). In a similar way the notion of a centre of origin has been banished from the literature, yet this concept is still clearly applicable in cases where general patterns are attributable to directional biotic

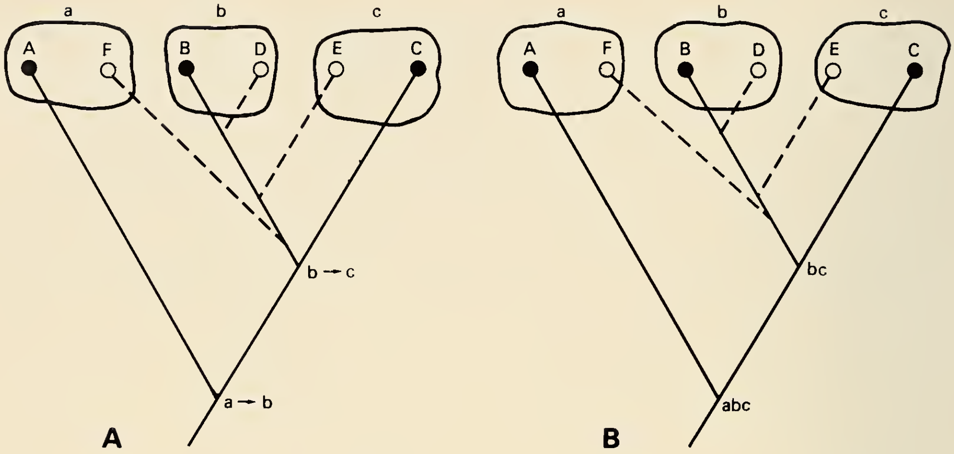

Fig. 12. Alternative hypotheses explaining the distribution of three taxa (A, B, C) in three areas (a, b, c), and tested by the discovery of new taxa (living or extinct) in the three areas (D, E, F). Neither hypothesis can be conclusively refuted. **A**, a dispersal explanation; taxon D is consistent with the dispersal explanation; taxon E can be explained by additional parallel dispersal, but suggests a vicariance explanation; taxon F can be explained by a reverse dispersal, but suggests a vicariance explanation: **B**, a vicariance explanation; taxa D, E, F can be explained by additional vicariance events, within areas b, c, and a respectively.

dispersal. Furthermore, it seems likely that this bias favouring vicariance may be due to the influence of geological theory. Patterson (1981) expresses the view (also Rosen, 1978) that historical geology cannot test biological area cladograms. But Platnick and Nelson (1978) have proposed the evidence of historical geology as a means of resolving causal explanations for a general pattern of area interconnections based on distributional data. In my view it would be false to pretend that current geological theories do not influence the way in which biogeographic problems are approached. As noted above, in the light of the prevailing geological model of breakup of a supercontinent (Pangaea) during the Mesozoic-Cainozoic to give the modern distribution of continents, an appraisal of vicariance as a preferable explanation for the biogeography of modern continental (including shelf) biotas seems very reasonable (the 'vicariance paradigm' of Nelson, 1976). Perhaps this results from a general preference for parsimony of hypotheses; that is, the potential of vicariance in this context to explain two or more events (continental breakup, plus dispersal of one or more groups of organisms), by one. However, vicariance is not necessarily an effective explanatory tool in other situations. During the middle Palaeozoic, for example, a plate tectonics interpretation suggests extensive continent collision between regions which had been separated by wide oceans during preceding geological periods. It is possible therefore that we have here completely the reverse, on a global scale, of the historical geological framework applicable to a biogeographic analysis of modern distributions. For modern faunas and floras in open marine situations the model of continental fragmentation during the Mesozoic-Cainozoic is not obviously relevant to an understanding of distribution patterns, and on a more local scale a similar situation has been argued by Holloway (1982) in the case of Melanesia, where emergence of new land areas and convergence of continents are thought to be the predominant features of recent geological evolution of the region.

The question to be asked therefore is what method of analysis is appropriate in those situations where it seems most unlikely that subdivision of an ancestral biota was

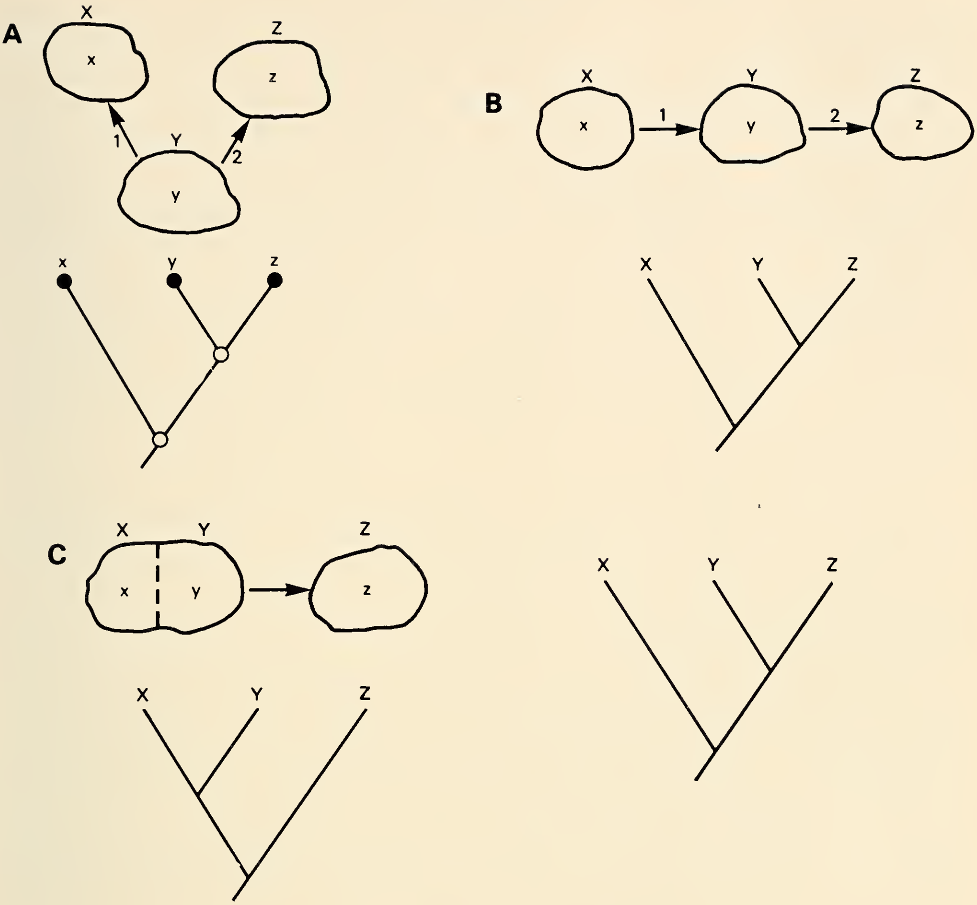

Fig. 13. Three ways in which a species (y), from which a new species (z) is derived by dispersal to colonize a new area or habitat, may be related to a third species (x) outside these areas. **A**, as a result of a previous dispersal to another area; **B**, as a result of a previous dispersal from another area (area cladogram shown); **C**, as a result of a vicariance event, which may have occurred before or after dispersal to area Z (alternative area cladograms shown). For discussion see text.

the predominant means of creating endemic faunas and floras. Holloway (1982) has argued that the biogeography of newly-formed land areas as in Melanesia must be seen in terms of dispersal and colonization from older land areas outside. In attempting to explain the first appearance of diverse early gnathostome faunas in many different regions at about the same time (Late Silurian/Early Devonian), I previously suggested (Young, 1981) that major groups may have evolved from ancestral forms widespread in shallow marine environments, as freshwater habitats were invaded. Both instances would be examples of colonialistic or vacuum biogeography in the sense of Platnick and Nelson (1978: 1). It is relevant to consider what relationships such colonizing forms might be expected to show to taxa of outside areas, and it seems obvious that any newly differentiated endemic species resulting from dispersal into a newly available area or habitat would have its sister group in the area or habitat from which it dispersed. For meaningful comparative analysis at least three taxa and areas must be considered (Fig.

13), and there seem to be only three ways in which outside relationships of the first species may develop:

a) it may have previously given rise to another dispersing species to a different area, which may be expressed in the cladogram of Fig. 13**A**. If there was no change in the area relationships (e.g. distance between areas, nature of barriers, etc.) then conversion to an area-cladogram in this case would seem to be spurious. In other words, it could be predicted that other species endemic to areas Y and Z would show outside relationships conforming to Fig. 13**B** or **C**, and the cladogram of Fig. 13**A** would conflict with a general pattern, and be inferred therefore to result from chance dispersal;

b) the relationship of the first species to a third species may be the result of prior dispersal from another area (giving, for the three areas, a sequential dispersal). As noted above, an area-cladogram in this situation will reflect the relative recency of dispersal events, which, if not due to chance, but to potentially identifiable causal factors (e.g. change in water currents, distance between areas), may form part of a general pattern;

c) the outside relationship of the first species may have resulted from a vicariance event (Fig. 13**C**). Unlike the previous case, there are here two possibilities depending on which event (vicariance or dispersal) occurred first. Either way a taxon cladogram converted to an area cladogram will reflect the relative recency (but not the degree or nature) of interconnections between areas. To the extent that other organisms were involved in both the vicariance and dispersal episodes, then this area cladogram may form part of a general pattern.

In the light of these considerations therefore, I suggest that where geological or other evidence points to directional dispersal across barriers as a predominant cause of disjunct distributions, the appropriate method of analysis is to develop hypotheses of relationship for endemic taxa in the areas concerned, convert the resulting taxon cladogram into an area cladogram, and then repeat the exercise with other groups such that a general pattern might be identified; in other words, the procedure advocated by Platnick and Nelson (1978). In such cases, where dispersal is regarded as the predominant mechanism, an assumption that there was a common ancestral biota (required under a vicariance model), can be replaced by an assumption that there was a centre of origin for those taxa involved in the analysis.

ANTIARCH BIOGEOGRAPHY

We may now consider again the cladogram of Fig. 2, to illustrate some of the points developed above using the distribution pattern of antiarchs as an example. Obviously, the first comment to be made is that by dealing with one group only, no reliable conclusions about general patterns can be drawn, and any inferences regarding area connections must be seen as tentative. Yet, as noted elsewhere (Young, 1984), it is appropriate that such analyses be undertaken, if only to present precise statements of the biogeographic implications of limited available data. In addition, where many sympatric taxa are involved, as appears to be the case within the antiarchs at the present level of analysis, it is possible that congruent patterns amongst antiarch subgroups might be identified. Previously (Young, 1981: 257), I suggested that any clear pattern of allopatric differentiation amongst the antiarchs was probably obscured by extensive dispersal. However, an examination of Fig. 2 suggests that only certain genera *(Bothriolepis, ?Remigolepis, ?Microbrachius)* have a markedly widespread distribution, which might be attributed to different dispersal capabilities of these forms. A detailed analysis, for example, of the distribution of the many species of *Bothriolepis* during the Middle/Late Devonian can thus be seen as a separate biogeographic problem, beyond the scope of this general discussion.

However the primary distribution of the four major antiarch subgroups during the Early Devonian is a matter for consideration. Regarding one of these, the asterolepidoids, it has been pointed out (Janvier and Pan, 1982; Young, 1984) that no representatives are known from south China before the Late Devonian. Considering that diverse fish faunas are known from many localities of Early and Middle Devonian age in the south China region (e.g. Pan, 1981), it seems unlikely that the absence of asterolepidoids is due to lack of preservation or discovery. Since the group is known from various Early and Middle Devonian localities elsewhere, it is reasonable to interpret the two genera known from south China *(Asterolepis, Remigolepis)* as late arrivals in the region. Whether this resulted from dispersal, or from range enlargement and vicariance, would depend on the nature of barriers between south China and other areas during the Late Devonian. Either way, it would seem that there was some change in the nature of these barriers, or with the dispersal capabilities of these late species, relative to the situation in the Early Devonian. The former alternative is perhaps supported by the fact that a marked provincial pattern amongst several groups of marine invertebrates during the Early Devonian was replaced in the Late Devonian by cosmopolitan faunas (e.g. Johnson and Boucot, 1973). This has been attributed to the development of extensive epeiric seas during Frasnian time.

As in the case of the placoderm *Phyllolepis* (Young, 1981), biostratigraphic evidence can be used to cope with a changing situation (palaeogeographic or otherwise) within the history of this group. Regarding the initial distribution ('centre of origin') of the asterolepidoid antiarchs, the earliest form so far recorded probably occurs in central Australia (Young, 1984), but there are good reasons (uncertainty regarding other areas not yet investigated, lack of morphological information permitting an adequate assessment of relationships) for not accepting this occurrence as significant. Considering the ten better-known genera included in Fig. 2, and applying Hennig's progression rule, gives Euramerica as their centre of origin; yet the displayed pattern is clearly not one suggesting that this rule would apply (cf. Fig. 8). The alternative vicariance model implies a widespread ancestral asterolepidoid in all four areas (Euramerica, Australia, Kazakhstan, south China), and in three when the biostratigraphic argument of late dispersal to south China is incorporated. The only reasonable conclusion on available evidence is that a specific area of origin for asterolepidoid antiarchs, if one existed, was in some region other than south China.

Turning to the other major antiarch subgroups (bothriolepidoids, sinolepids, yunnanolepids), south China has been inferred to be an evolutionary centre (Young, 1981), since much of the early differentiation within these groups occurred in this region (Fig. 2). However this general observation requires closer scrutiny. The bothriolepidoids, in contrast to the asterolepidoids, are well represented in the early Middle Devonian of south China (e.g. *Dianolepis, Bothriolepis*), whereas the latter genus only became widespread (Europe, Russia, Greenland, North America, etc.) during the Late Devonian. Again, decreased isolation for the south China region is indicated, and again biostratigraphic evidence suggests a change in the nature of barriers, or in dispersal capabilities, between Middle and Late Devonian time. Before such changes occurred, several more primitive bothriolepidoid taxa differentiated in the south China region, and the same applied for their presumed sister group (the sinolepids). Applying the progression rule gives south China as the centre of origin for this monophyletic group, and if the Australian sinolepid and the Euramerican *Microbrachius* are attributed to later dispersal, then the early vicariance history of the group could be interpreted as confined to the south China region, approximating a pattern of the type in Fig. 8**D.** At least for the Australian sinolepid, which is Late Devonian in age, a case for dispersal might be argued. Alternatively, the involvement of Australia at two positions in the cladogram could indicate that the common ancestor for the group was distributed in both regions, giving a pattern similar to (but more complex than) that illustrated in Fig. 8**E**. This example illustrates the arbitrariness of decisions about vicariance or dispersal mechanisms based on a single group, and also the problems of dealing with fossil data involving incomplete sampling through more than one area pattern (reflecting different palaeogeographies at different times). For resolution it would seem necessary to rely on reciprocal illumination using geological or biostratigraphic data, although neither is yet particularly helpful in this case. Nevertheless, considering together the available distributional data for the asterolepidoids, a vicariance explanation for the differentiation of the two groups is indicated, as argued by Janvier and Pan (1982). Thus the area of origin for the bothriolepidoids (? plus sinolepids) can be specified as including south China, and possibly other areas, of which the most likely is Australia.

The last major subgroup (yunnanolepids) includes remarkably primitive forms which have only been recorded from the Early Devonian (or older) of south China. Janvier and Pan (1982: 388) question whether this means that south China was their centre of origin, but given their known distribution the only reasonable assumption is that the group evolved in place (that is, that their most recent common ancestor also occurred only in south China). The fact that this, the most primitive known group of antiarchs, is restricted to south China, means that application of the progression rule for antiarchs generally also gives their origin as south China. It could again be suggested that there is a biostratigraphic argument supporting this notion (the early antiarchs in south China are considerably older than known elsewhere; Pan, 1981), but in this case the argument is not necessarily valid, and depends on questions of relationship at the base of the antiarch cladogram. Thus, if yunnanolepids are monoplyletic, and the Late Silurian antiarchs from south China (Pan, 1981) can be shown to belong to this group, then this gives a minimum age of Late Silurian for ancestral euantiarchs also (Young, 1984:77), even though they are not recorded until somewhat later (perhaps late Lower Devonian; see Young, 1984). On these theoretical grounds therefore the biostratigraphic argument pointing to a south Chinese origin for all antiarchs would not be valid. On the other hand, if yunnanolepids are paraphyletic, with some members more closely related to euantiarchs (on pectoral fin structure *Phymolepis* is a possible candidate; see Fig. 2), then south Chinese origins for both euantiarchs and antiarchs generally would be indicated, and the biostratigraphic argument would provide supporting evidence. Clearly the morphology and relationships of the Late Silurian antiarchs of south China are of central importance here, as is the position of sinolepids on the cladogram. If sinolepids (in accordance with earlier schemes) were regarded as the sister group of other euantiarchs, then a similar conclusion would be indicated (an implied secondary biostratigraphic argument involving late dispersal of sinolepids into Australia would be subject to independent investigation). However, based on my current appraisal of antiarch interrelationships (Fig. 2), and assuming until there is good evidence to the contrary that yunnanolepids are a monophyletic group, the available evidence indicates a widespread distribution for both ancestral antiarchs and ancestral euantiarchs.

To summarize, the following areas of origin for the major monophyletic groups of antiarchs are suggested: asterolepidoids, an area including part of all of Euramerica, Kazakhstan, and Australia, but excluding south China; bothriolepidoids plus sinolepids, south China, or south China plus Australia; yunnanolepids, south China; euantiarchs and antiarchs, cosmopolitan. On the centre of origin concept generally, Janvier and Pan (1982: 387) have noted aspects in common with the idea of ancestral species or groups, the recognition of which depends on the absence of derived characters, and earlier stratigraphic age. But as stated in the previous section, where dispersal is the cause of general patterns, the centre of origin concept clearly has validity, and, as is clear from the preceding discussion, where the primary distribution of a group has been enlarged by secondary dispersal, one can also develop arguments to specify that primary distribution or area of origin.

Since the issue of completeness of the fossil record appeared in several contexts in the preceding discussion, it is appropriate to conclude by briefly considering the nature of the fossil record of the antiarchs. Regarding future discoveries, it is of course true that 'no one knows what may be found' (Patterson, 1981: 463), and this applies particularly to many areas where there has been little or no search for Devonian vertebrates. But other areas are better known, and some predictions regarding future discoveries might be made. Thus, over the many years that Devonian fishes of Europe have been studied, the antiarch *Bothriolepis* has not been found in strata older than late Middle or early Late Devonian. Similarly, after some two decades during which the Early and Middle Devonian antiarchs of south China have been investigated, no reports of members of the Asterolepidoidei have withstood re-evaluation, the two known representatives *(Asterolepis, Remigolepis)* being Late Devonian in age. Assuming that the presence of these latter forms in south China is due to dispersal (which is demonstrated by sympatry, regardless of differences in age), the known fossil record shows that this dispersal originated outside the areas occupied by the earlier faunas, and gives an indication of the approximate time (late Middle Devonian) when barriers to such dispersal ceased to operate. It would seem that any argument that such biostratigraphic evidence should not be utilized on the grounds that future discoveries (in this case Early Devonian asterolepidoids in south China) might change the pattern, can be rejected as unscientific, because it attributes the observed pattern to chance alone, and such explanations cannot be subjected to further scientific investigation.

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